

# AN INVESTIGATION OF MORPHOLOGICAL EVIDENCE SUPPORTS THE RESURRECTION OF *PYRROCOMA SCABERULA* (ASTERACEAE: ASTEREAEE)

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## ABSTRACT

Field data were gathered from 31 wild populations of *Pyrrocoma liatrisformis* sensu lato (Asteraceae, Astereae). These are measures of degree of tomentosity and glandularity, number of lateral inflorescence branches, number, length and width of flower heads, width of phyllaries, and width of the lowest leaf of the inflorescence. Principle components analysis and univariate statistics of these characters reveal non-uniformity in the morphology of *P. liatrisformis* sensu lato, with two identifiable morphologies corresponding to geographical range, as divided into the Palouse grasslands on the one hand and grasslands of the Snake River Canyons/Camas Prairie region on the other. The plants of the latter geographical range are represented by the type of *Pyrrocoma scaberula*, hitherto synonymized under *P. liatrisformis* since the original publication of these names in 1909. The segregation of populations into a resurrected *P. scaberula* leaves *P. liatrisformis* sensu stricto a much rarer and an even more threatened species. Conservation implications of this taxonomy are discussed.

## RESUMEN

Se colectaron datos de 31 poblaciones salvajes de *Pyrrocoma liatrisformis* sensu lato (Asteraceae, Astereae). Estos datos representan medidas del grado de tomentosidad, glandulosidad, número de ramas laterales de las inflorescencias, longitud y anchura de la cabezuela de flores, grosor de los filarios, y anchura de la hoja inferior de la inflorescencia. Los análisis de componentes principales y los análisis univariantes revelaron falta de uniformidad en la morfología de *P. liatrisformis* sensu lato, y también dos morfologías identificables correspondientes a la siguiente división geográfica: Los pastizales de Palouse y los pastizales del cañón Snake River / Pradera de Camas. Las plantas de la segunda región geográfica están representadas por el tipo *Pyrrocoma scaberula*, previamente bajo el sinónimo de *P. liatrisformis* desde la publicación original de estos nombres en 1909. La segregación de esta población, con la resurgida *P. scaberula*, deja a la especie *P. liatrisformis* sensu stricto más rara y aún más amenazada. Se discuten las implicaciones para la conservación de esta taxonomía.

KEY WORDS: *Pyrrocoma*, Asteraceae, Astereae, Palouse, Snake River Canyon, Camas Prairie, principle components analysis

## INTRODUCTION

Members of the genus *Pyrrocoma* Hooker (Asteraceae: Astereae) are taprooted, herbaceous perennials with basal rosettes and leafy stems topped by one to several flower heads with yellow ray florets. The genus is endemic to western North America, and includes 26 taxa as circumscribed in the most recent treatment (Bogler 2006). Between Hall's monograph of the genus in 1928 and Mayes' monograph in 1976, *Pyrrocoma* was generally merged along with numerous other genera under *Haplopappus*. Recent morphological and molecular work suggests that such a broad use of *Haplopappus* results in a polyphyletic assemblage (Clark et al. 1980; Morgan 1992).

Edward L. Greene presented the names *Pyrrocoma liatrisformis* and *Pyrrocoma scaberula* in a single publication in 1909, and subsequently, the latter has been treated as a synonym of the former (Hall 1928, Mayes 1976, Hitchcock & Cronquist 1973). *Pyrrocoma scaberula* was represented in its type collection by poor material, and until the 1990's, further collections from populations in the region of the type locality were unknown. Upon the availability of these specimens, it became apparent that plants from the region of *P. scaberula* consistently share many of the morphological traits described for and apparent in the type of *P. scaberula*. These traits appear to make them morphologically and geographically separable from typical *P. liatrisformis*.



*Pyrrocoma liatrisformis* sensu lato is currently placed on the United States Fish and Wildlife Service's Species of Concern list. At the time of its first listing as a conservation priority, the species was thought to be found primarily in the Palouse grasslands, but in recent years, numerous large populations of the species in its broad sense have been located in the canyon grasslands in the vicinity of the Snake, Clearwater and Salmon Rivers (Mancuso 1997). These newly found populations all share morphological characteristics with the type of *P. scaberula*, which was also collected in this more southerly region (near the town of Forest, Nez Perce County, Idaho).

The present study aims to test 1) the morphological coherence of populations of *Pyrrocoma liatrisformis* sensu lato, 2) whether any distinct morphologies correlate to geographical range, 3) whether all populations can be unambiguously assigned to either of the hypothesized morphological entities, and 4) whether a portion of the populations are comparable to the type of *P. scaberula* and so can be assigned that name.

#### METHODS

Plants of both of the hypothesized morphologies were studied in the field in 31 populations. Seventeen populations were sampled the Palouse grasslands in Whitman County, Washington, and Latah and northern Nez Perce Counties, Idaho. Fourteen populations were sampled in grasslands of the Snake River Canyon system and adjacent Camas Prairie in Asotin County, Washington, southern Nez Perce, Idaho and Lewis Counties, Idaho. These 31 populations constitute more than one third of the 91 known extant occurrences (K. Gray, pers. com., Kemper 2005) from throughout most of the known range of *Pyrrocoma liatrisformis* sensu lato. In total, 322 plants were studied in the field, 201 of them from the Palouse grasslands, and 124 from the canyon/Camas Prairie grasslands.

Two additional populations were studied based on herbarium specimens only. Both of these populations were newly discovered in 2005 by other collectors and were not seen by the authors until after the conclusion of field work for the present study. These specimens were included in the study because they represent populations in areas where *Pyrrocoma liatrisformis* was previously not known to grow (one specimen from Wallowa County, Oregon, and two specimens from Washington County, Idaho, both located far south of the Palouse grasslands).

Plants in the field surveys were chosen randomly on intervals along walkabouts following contours of the topology so as to sample plants on any occupied slopes, aspects and soil/moisture conditions. Eight variable morphological characters were assessed based on the hypothesis that they are informative of genetic lineage and hence taxonomic placement. Two of these characters are qualitative: 1) pubescence (tomentose, non-tomentose or intermediate), 2) glandularity (strongly, weakly or intermediate). Six characters used are quantitative: 3) number of lateral inflorescence branches longer than 1 cm, 4) number of flower heads, 5) length of flower heads (from the base of the lowest closely ensheathing phyllaries up to the tips of the highest-positioned phyllaries; three heads, the lowest highest and a middle one were measured), 6) width of flower heads (non-pressed; same heads measured for length), 7) width of the phyllaries (measured among the second or third ranks of phyllaries on the same heads as measured for head length and width), and 8) width of the lowest leaf of the inflorescence. All quantitative characters appear not to be interdependent, with no correlation between them having an  $r^2$  value higher than 0.463 (head width with phyllary width).

From large populations, voucher specimens (one fertile stem each) were gathered for every sampled plant. Plants from small populations were vouchered nondestructively by use of digital photographs, taken with a ruler for scale. Photos will be archived in both digital and printed format at the Stillinger Herbarium, University of Idaho, where voucher specimens will be deposited as well.

Quantitative morphological characters were entered as continuous variables in principle components analysis (PCA) run on PCORD (MjM Software Design). Characters 3 and 4 were discarded from the PCA owing to the large number of aborted branches and heads, which was perhaps due to the severe drought that occurred throughout the study area in the year of the field season. Correlations of characters with the first and second axes were sought to determine which characters contribute most to any clustering pat-



terns. Points in the PCA graphs were matched to their geographical range, pubescence type, and degree of glandularity to visually seek any correlations between the discrete and quantitative variables.

Means and standard errors of morphological characters and hypothesis tests were generated using JMP Version 3.2.6 for Windows (SAS Institute). Correlated discontinuities were sought using the ranges and means of both individual plant data and population means arrayed by geographical range, pubescence type and degree of glandularity.

High-resolution images were examined of the type specimens of *Pyrrocoma liatrisformis*, *Pyrrocoma scaberula*, and *Pyrrocoma suksdorfii* E. Greene, which is the third name synonymized under *P. liatrisformis* in all treatments since the publication of all three names by E. Greene. All three are housed at the U.S. National Herbarium, and may be viewed at the type specimen register at <http://ravenel.si.edu/botany/types>.

## RESULTS

All eight morphological characters reveal non-uniformity within *Pyrrocoma liatrisformis* sensu lato (Table 1). Within- and among-population variation is seen in all quantitative variables, but pubescence type and degree of glandularity were strongly uniform within populations.

The principle components analysis reveals clusters of populations, separated along axis one, which accounted for 81.88% of the variation. Axes two through four had broken-stick Eigenvalues higher than their actual Eigenvalues, and are thus not further considered. Correlation coefficients were greatest with axis one for phyllary width (-0.5147) and head length (-0.5046).

For pubescence type, all populations scored for the tomentose and intermediate types overlap in the right cluster in the PCA graph, along with two populations scored as non-tomentose (populations KS and GR, Fig. 1). All other non-tomentose populations appear in the left cluster. Similarly, populations scored as weakly and intermediately glandular overlap within the right cluster, along with two of the populations scored for strong glandularity (populations KS and GR). The left cluster correlates to populations of the canyon/Camas Prairie grasslands, while all plants of the Palouse grasslands cluster on the right.

When plants are assigned to geographical range (Palouse grassland versus canyon/Camas Prairie grassland) without considering population means, the ranges of the quantitative variables are overlapping to varying degrees, but are all significantly different (Table 1). Population means assigned to geographical range reveals far less overlap in head length, head width, phyllary width, and leaf width, but no appreciable separation in lowest and highest values is seen in number of lateral branches and number of flower heads (Table 2). Two outlier low values for population means of the canyon/Camas Prairie plants occur for head length and phyllary width; when these outliers are disregarded, there is no overlap in the ranges for population means in phyllary width, and very little for head length.

Plants of the Palouse grasslands in all but two populations were strongly or intermediately tomentose, with the tomentum being lanate and distributed most densely on the phyllaries, but often throughout the entire plant. Plants of the canyon grasslands and two proximal populations on the Palouse (Kramer Prairie and Gross Road) often have harsh, curled hairs on the stems and inflorescence branches, but never on the phyllaries, and the hairs are never lanate. Degree of glandularity was distributed among populations almost perfectly concomitantly with the occurrence of tomentum, the exceptions being that some Palouse populations could be strongly tomentose but intermediately glandular, or intermediately tomentose and weakly glandular. All plants of the canyon/Camas Prairie grasslands were strongly glandular, with resinous-punctate glands being distributed most strongly on the phyllaries and usually also on the cauline leaves. Any glands among Palouse plants were limited to the phyllaries. Among the quantitative variables, the Palouse plants had a greater number of lateral inflorescence branches, more numerous flower heads, shorter and narrower heads, narrower phyllaries and narrower cauline leaves (Table 1).

The Kramer Prairie (KS) and Gross Road (GR) populations, though located on the Palouse grasslands, share the lack of tomentum and strong glandularity of the canyon/Camas Prairie plants. However, they are attributable to the Palouse-type morphology based on (means and standard errors, values for KS preceding



TABLE 1. Means, standard error, and ranges of quantitative morphological characters for plants assigned to geographical range. Asterisks following the characters indicate the significance of the ANOVAs comparing per-plant values by geographical range.

Character	Geographical range	
	Palouse	Canyon/Camas Prairie
Number of lateral branches*	2.39 ± 0.16(0–17)	1.78 ± 0.19(0–7)
Number of heads**	7.57 ± 0.34(1–57)	5.67 ± 0.39(1–33)
Head length (mm)***	11.79 ± 0.12(8–17(–18.5))	14.22 ± 0.14(9–)11–21)
Head width (mm)***	6.56 ± 0.10(4–10(–11))	8.71 ± 0.11(6–14)
Phyllary width (mm)***	1.90 ± 0.03(1–3(–3.5))	2.83 ± 0.04(1.5–)3–5)
Leaf width (mm)***	7.23 ± 0.21 (4–14)	10.45 ± 0.21(4–) 6–19)

TABLE 2. Ranges of population means of quantitative morphological characters for plants assigned to geographical range. Values in parentheses are single-observation outliers.

Character	Geographical range	
	Palouse	Canyon/Camas Prairie
Number of lateral branches	0.5–6.4	0.0–3.17
Number of heads	1.6–14.0	3.0–15.0
Head length (mm)	10.3–13.9	(8.5–)13.8–15.1
Head width (mm)	5.8–8.7	7.4–11.1
Phyllary width (mm)	1.4–2.3	(1.4–)2.3–3.3
Leaf width (mm)	5.0–9.4	9.3–15.4

in each case): head length ( $12.63 \pm 0.35$ ;  $12.53 \pm 0.35$ ), head width ( $6.58 \pm 0.23$ ;  $6.66 \pm 0.18$ ), phyllary width ( $2.29 \pm 0.73$ ;  $2.27 \pm 0.12$ ), and leaf width ( $7.44 \pm 0.57$ ;  $7.55 \pm 0.59$ ), though their mean number of lateral branches ( $0.53 \pm 0.29$ ;  $1.36 \pm 0.43$ ), and number of flower heads ( $6.82 \pm 0.78$ ;  $5.64 \pm 0.71$ ) fell near the means of the canyon/Camas Prairie plants.

The type specimen of *Pyrrocoma liatrisformis* (C.V. Piper s.n. 29 August, 1903, Pullman, Washington, US) shows a tomentose plant lacking conspicuous glandularity. The number of lateral branches average 6.5 between the two stems, and the number of flower heads averages 9.0. Head length averages 12.03 mm (6 heads), phyllary width ranges 1.5–2.0 mm, and width of the lowest leaves of the inflorescence is 7.5 mm. The type of *Pyrrocoma scaberula* (A.A. Heller 3469, 29 July, 1896, Forest, Nez Perce County, Idaho, US) is a non-tomentose plant with conspicuous glands on the phyllaries. Each of the 4 non-damaged stems bears no lateral branches and a single flower head. The heads are 12.5 to 14.5 mm long, and the phyllaries are 2.2 mm wide or greater. The width of the cauline leaves is narrow (mean of 4.2) compared to other plants from the canyon/Camas Prairie examined in the present study. The type of *Pyrrocoma suksdorfii* is a tomentose plant with no conspicuous glandularity. The number of lateral branches average 2.0, and the number of heads per stem is 4.7. Head length ranges 10–11.5 mm, the phyllaries are under 2.0 mm long, and the cauline leaf width averages 6.0 mm.

DISCUSSION

Qualitative and quantitative characters reveal that *Pyrrocoma liatrisformis* sensu lato is morphologically non-uniform, both within and among populations. Sorting plants and populations into geographical range between the Palouse grasslands on the one hand and the canyon/Camas Prairie grasslands on the other reveal that this variation is nonrandom and is correlated to geographical range. While geographical range does not account for all variation, there are clearly two arrays of morphology that are each coherent within their own geographical range. Further, narrow discontinuities in the arrays of morphological variation for half of the quantitative characters (Head length, Phyllary width and Leaf width) are concomitant when population



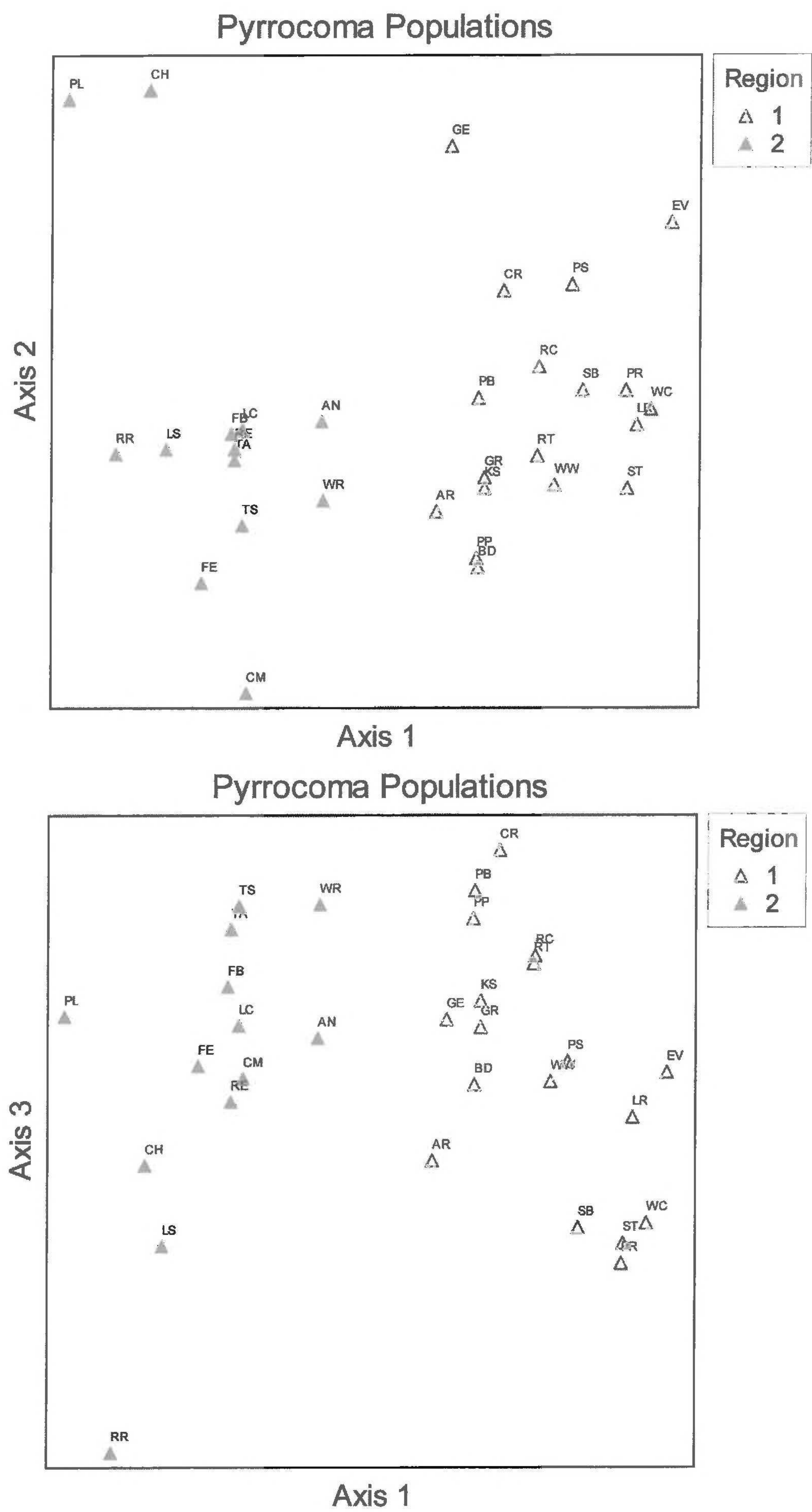


FIG. 1. PCA graph showing axes 1 versus 2, and 1 versus 3, respectively. The solid triangles represent populations of the canyon/Camas Prairie region. The open triangles represent the Palouse region.



means are sorted by geography. While there is considerable overlap in the remaining quantitative characters, and two of the Palouse populations break with their co-distributed populations in the qualitative characters, the distinctions among the most strongly diagnostic quantitative characters (Phyllary width, Head length, Head width and Leaf width) allows their placement within the Palouse morphology.

In the initial herbarium-based investigation comparing the Palouse and canyon/Camas Prairie morphologies within *Pyrrocoma liatrisformis* sensu lato, a greater spread in means was found for number of lateral branches ( $3.86 \pm 0.73$  versus  $1.54 \pm 0.49$ , respectively) and number of flower heads ( $11.89 \pm 1.86$  versus  $5.38 \pm 1.07$ ). Extreme drought occurred throughout the study area in the year of the field work, with very little precipitation falling in the preceding winter and spring, when normally the bulk of annual precipitation falls in both the Palouse and canyon/Camas Prairie regions. This suggests that under normal conditions, these two quantitative characters would be more diagnostic than is suggested by the data gathered from the field in 2005. Plants in all populations visited had a portion of their lateral branches and flower heads aborted, as evidenced by the number of small, distorted branches and heads that senesced without maturing flowers or fruits.

Examination of the type specimens of *Pyrrocoma liatrisformis*, *Pyrrocoma scaberula*, and *Pyrrocoma suksdorfii* reveal that these plants are comparable to others collected from the same geographical regions in the present study. The observed morphologies of the Palouse grassland populations are clearly represented by the types of *Pyrrocoma liatrisformis* and *Pyrrocoma suksdorfii*. The latter shows no appreciable distinction from the former, and its morphological characters fit within the ranges observed in the field for the Palouse populations in general, thus the name *P. suksdorfii* appears to be correctly synonymized under *P. liatrisformis*. The type of *P. scaberula* fits well within the observed range of morphologies of the canyon/Camas Prairie populations (except in the width of the cauline leaves, which are within the range of the Palouse populations, and the anomalous single flower heads per stem, which was rarely observed in both geographical ranges). Thus, the type of *Pyrrocoma scaberula* appears to be representative of all populations of the canyon/Camas Prairie region.

#### KEY TO PYRROCOMA LIATRIFORMIS AND PYRROCOMA SCABERULA

1. Plants mostly heavily lanate-tomentose throughout, sometimes only on and near the flower heads; resinous-punctate glands usually absent or inconspicuous; population means of flower head length 10–13.8 mm; phyllaries 1.4–2.3 mm wide; population means for width of the lowest leaf of the inflorescence up to 9.3 mm; plants occurring in the Palouse grasslands \_\_\_\_\_ ***Pyrrocoma liatrisformis***
1. Plants hispid, any longer hairs harsh and firm, never lanate; resinous-punctate glands conspicuous, especially on the phyllaries; population means of flower head length 13.8–15.1, very rarely less; phyllaries 2.3–3.3 mm (very rarely less); population means for width of the lowest leaf of the inflorescence more than 9.3 mm; plants occurring south of the Palouse grasslands \_\_\_\_\_ ***Pyrrocoma scaberula***

The degree of variation within *Pyrrocoma liatrisformis* and *Pyrrocoma scaberula*, the overlap in certain characters, and the narrow discontinuities in both the geographical ranges and among the most diagnostic quantitative characters suggest a close relationship between the two. While the coherence of morphologies within the Palouse and canyon/Camas Prairie geographical ranges suggests that it is highly unlikely that the two species are randomly polyphyletic to each other, it is possible that one species is derived from the other (one monophyletic and the other paraphyletic), rather than both being derived from a now extinct common ancestral race (both monophyletic). Further, hybridization may have occurred giving rise to intermediate populations. The two Palouse populations here assigned to *Pyrrocoma liatrisformis* which have the non-tomentose and strongly glandular condition of *Pyrrocoma scaberula* suggest either hybridization, or that these populations might actually be closer related to *P. scaberula*. It is also possible that specific taxonomic rank may be unmerited for *P. scaberula*, such that it would be best recombined as a variety of *P. liatrisformis*. An ongoing molecular study will address these questions, assaying AFLP loci from all plants measured in the field in the present study.

Population means of head length, phyllary width and leaf width, along with the strong tendencies toward



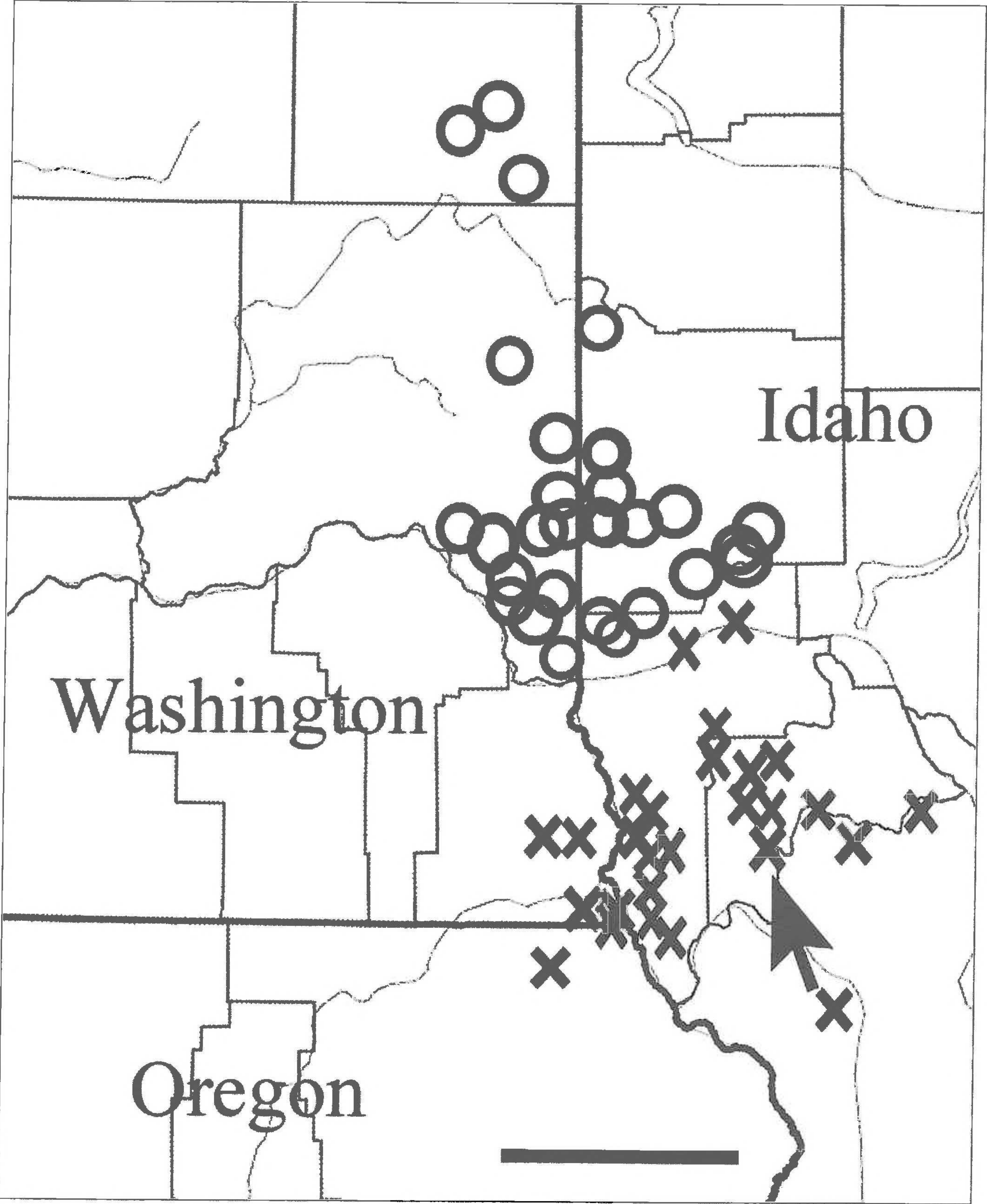


FIG. 2. Map showing locations of surveyed populations and additional herbarium specimens. Circles represent *Pyrrocoma liatriformis* and X's represent *Pyrrocoma scaberula*. The arrow points to the type locality of *Pyrrocoma scaberula*. The scale bar at the bottom represents 50 km. Not shown is the single known population in Washington County, Idaho, well to the south of the map range.



character states in the other morphological variables allow the unambiguous assignment of populations to either *Pyrrocoma liatrisformis* or *P. scaberula*. Thus, the segregation of the relatively common and widespread *P. scaberula* leaves *P. liatrisformis* sensu stricto as a very rare and highly threatened species. Several populations of *P. scaberula* are over 1,000 individuals (K. Gray, pers. comm.) and occupy large tracts of natural grassland, and the newly discovered populations in Wallowa County, Oregon and Washington County, Idaho suggest that additional populations may await discovery in the poorly explored grasslands of Hells Canyon in the intervening area. In contrast, nearly all of the populations of *P. liatrisformis* are less than 500 individuals, and its potential habitats are all much smaller tracts surrounded by agricultural fields (Fig. 2). Intensive surveys in 2005 for additional populations in the Palouse grasslands by the present authors, as well as by the Idaho Conservation Data Center (K. Gray, pers. comm.) and Washington Natural Heritage Program (T. Kemper, pers. com.) in the same year make it highly unlikely that additional large populations will be discovered. Thus, *P. liatrisformis* sensu stricto is vulnerable to extinction and should be protected accordingly.

#### ACKNOWLEDGEMENTS

This research was supported by funding from the U.S. Fish and Wildlife Service and Bureau of Land Management. We are very grateful for the enthusiastic assistance from the Idaho Conservation Data Center, the Stillinger Herbarium, University of Idaho, the Ownbey Herbarium, Washington State University, and especially to Karen Gray for the seed idea, and we thank Federico Osorio for the Spanish translation. David J. Bogler and an anonymous reviewer provided helpful comments.

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